Great Basin Naturalist 54(1), © 1994, pp. 71–78

PERSISTENT POLLEN AS A TRACER FOR HIBERNATING BUTTERFLIES: THE CASE OF *HESPERIA JUBA* (LEPIDOPTERA: HESPERIIDAE)

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ABSTRACT.—Pollen grains of plants with well-defined flowering seasons may persist on insects through episodes of dormancy, such as hibernation. When readily recognizable and possibly confounding taxa can be excluded, these pollen grains can serve as direct evidence of life-history phenomena that are notoriously difficult to verify in the field. Pollen of the autumn-flowering composite *Chrysothamnus nauseosus* was used to demonstrate that the common montane skipper, *Hesperia juba*, hibernates as an adult in the Sierra Nevada. This is the first demonstration of adult overwintering in a temperate-zone hesperiid and may represent the smallest butterfly known to overwinter in a cold climate.

Key words: pollen carryover, hibernation, phenology, body size, Hesperia juba, Chrysothamnus nauseosus, Nymphalis antiopa.

Many life-history phenomena of insects, including seasonal dormancy and migration, can be inferred from phenological data but are notoriously difficult to demonstrate directly in the field; the animals are too few and/or difficult to find. Many Holarctic nymphaline butterflies have been suspected of hibernation since the 18th century, but there is still no direct evidence in many of them. Direct evidence requires either the post-hibernation recovery of individuals marked the previous season (or otherwise identifiable), or the discovery of hibernating individuals and the demonstration that they are able to survive winter in situ and enter the reproductive pool in spring. Despite the rarity of such evidence, the hypothesis of adult hibernation is repeated uncritically in most modern accounts of nymphaline biology. It is much more difficult to persuade anyone that a butterfly belonging to a lineage hitherto unsuspected of hibernation in fact overwinters as an adult.

Kettlewell (1961) and Kettlewell and Heard (1961) were able to use a radioactive particle originating from an atmospheric nuclear test in the Sahara Desert to trace the origin of a migrant moth (*Nomophila noctuella* Schiff., Pyralidae) collected in Britain. Pollen grains are a more prosaic surface contaminant of insect specimens which under favorable circumstances can serve the same purpose. Demonstration of even a single adherent grain of pollen of an autumn-flowering plant on a spring-collected insect could document the overwinter survival of that individual. There seems to be no prior documentation of such long-term pollen persistence. We applied the concept to the Californian skipper, *Hesperia juba* Scudder (Hesperiidae), which has been suspected of adult hibernation, using as our index pollen species the composite shrub *Chrysothamnus nauseosus* (Pall.) Britton, with encouraging results.

The difficulty of verifying hibernation is illustrated by Shapiro's previous studies of *H. juba* (Shapiro 1981). He marked 104 individuals at Donner Pass in the Sierra Nevada in September 1979. In June 1980 he captured 18 individuals in the same area, but none was marked. This was an unusually large-scale attempt at a direct demonstration of overwintering; hibernating nymphalids seldom occur at similar densities. Shapiro noted that the negative result was uninterpretable; the only meaningful result would have been the capture of one or more marked specimens.

NATURAL HISTORY OF *HESPERIA JUBA*

Hesperia juba is a common and widespread montane skipper in California and adjacent states. Despite its commonness, its life history remains very poorly known. MacNeill (1964) described the early stages based on laboratory

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rearing but did not understand its phenology. Misled by pooling data from a very heterogeneous mix of localities, he wrote that

> the adults are present from April through October, with some variation according to locality; evidently emergence is rather continuous and there are no distinct seasonal broods.

Emmel and Emmel (1973) recorded two distinct flights in southern California (April–June and August–September); and all subsequent local or regional data, from Oregon (Dornfeld 1980) to Baja California (Brown et al. 1992), have been similar. Shapiro (1979) was the first to point out that the phenology of *H. juba* was not only well defined but very unusual for a skipper. He presented eight years of Donner Pass data (1972–79) resulting from a biweekly sampling program. This study is now in its 21st year, and the pattern evident in 1979 has continued with great consistency (Table 1). *Hesperia juba* occurs at 5 of the 10 stations on Shapiro's northern California transect and is definitely resident at 4 of these; at all 4 it is spring/autumn bivoltine with slight variation in phenology, over an altitudinal range of 1500–2750 m.

No other hesperiine skipper is bivoltine at Donner Pass (2100 m) or higher, and no other skipper flies either so early in spring or so late in autumn. The only other bivoltine hesperiine in the region is *Polites sabuleti tecumseh* (Grinnell) at the lower limits of its range (1500 m on both the Sierran east and west slopes, but only irregularly bivoltine on the west). It is only about 60% the size of *H. juba*, but even so it emerges later in spring (much later at Donner Pass, where it is univoltine). At Donner, *H. juba* is often one of the first species to fly after snowmelt, along with the presumably adult-hibernating nymphalids and pupal-hibernating *Celastrina argiolus echo* (W.H. Edwards)(Lycaenidae) and *Pontia occidentalis* (Reakirt)(Pieridae). These and other circumstances described in Shapiro (1979) led to the suggestion that *H. juba* hibernates as an adult. Nonetheless, Scott (1986) ignored this suggestion, proposing instead that *H. juba* overwintered as a larva.

An overwintering larva would not be expected to feed and grow under a snowpack that normally persists for 6–7 months. Thus, growth would be limited to the periods of good weather between autumn flight and onset of snow, and between snowmelt and some (pupation) time before the spring flight—in all, a few weeks. Skippers grow slowly even under seemingly optimal conditions.

TABLE 1. Phenology of *Hesperia juba* at Donner Pass (2100 m) in the Sierra Nevada of California, based on roughly biweekly sampling, 1972–92.

Year	First flight	Second flight	N_1[a]	N_2[b]
1972	v.24–vi.7	viii.10–x.4	64	78
1973	not seen	ix.7–x.5	—	—
1974	vi.9	viii.24–ix.27	75	75
1975	vi.11	ix2.–ix.30	82	82
1976	v.14–vii.1	vii.20–x.8	49	96
1977	vi.4	ix.2–ix.23	90	90
1978	vi.14–vii.1	viii.15–x.23	45	61
1979	vi.1–vii.12	ix.4–ix.30	54	96
1980	vi.7–vii.5	ix.4–ix.27	61	89
1981	vi.7–vi.21	viii.6–ix.6[c]	36	50
1982	vi.23–vii.9	ix.1–ix.20	54	70
1983	vi.5–vii.12	viii.30–x.26	48	85
1984	v.27–vi.20	ix.6–ix.22	78	102
1985	v.23–vi.19	viii.20–x.5	63	90
1986	v.17–vi.15	ix.4	81	110
1987	vi.2	viii.11–ix.17	70	70
1988	iv.26–v.14	viii.19–ix.22	97	115
1989	v.20–vi.18	viii.28–x.8	72	101
1990	v.12–vi.2	ix.5–ix.18	95	116
1991	vi.2–vii.5	ix.4–x.12	61	94
1992	iv.28–vi.8	viii.22–ix.26	79	116

[a]Number of days from last observation of first flight to first observation of second flight.
[b]Number of days from first observation of first flight to first observation of second flight.
[c]No late-September sample taken (investigator out of country).

While attempting to carry various stages of *H. juba* overwinter in the laboratory, we reared a single larva from egg to (male) adult in 83 days at a continuous temperature of 26°C under outdoor photoperiod on growing *Poa* sp. (Gramineae). This individual developed without interruption (except for molts). We estimate the time available for circumhibernal larval development in an average year to be on the order of 75–85 days, nearly all with night temperatures below freezing and with afternoons reaching 20°C for perhaps 2–3 hr/day!

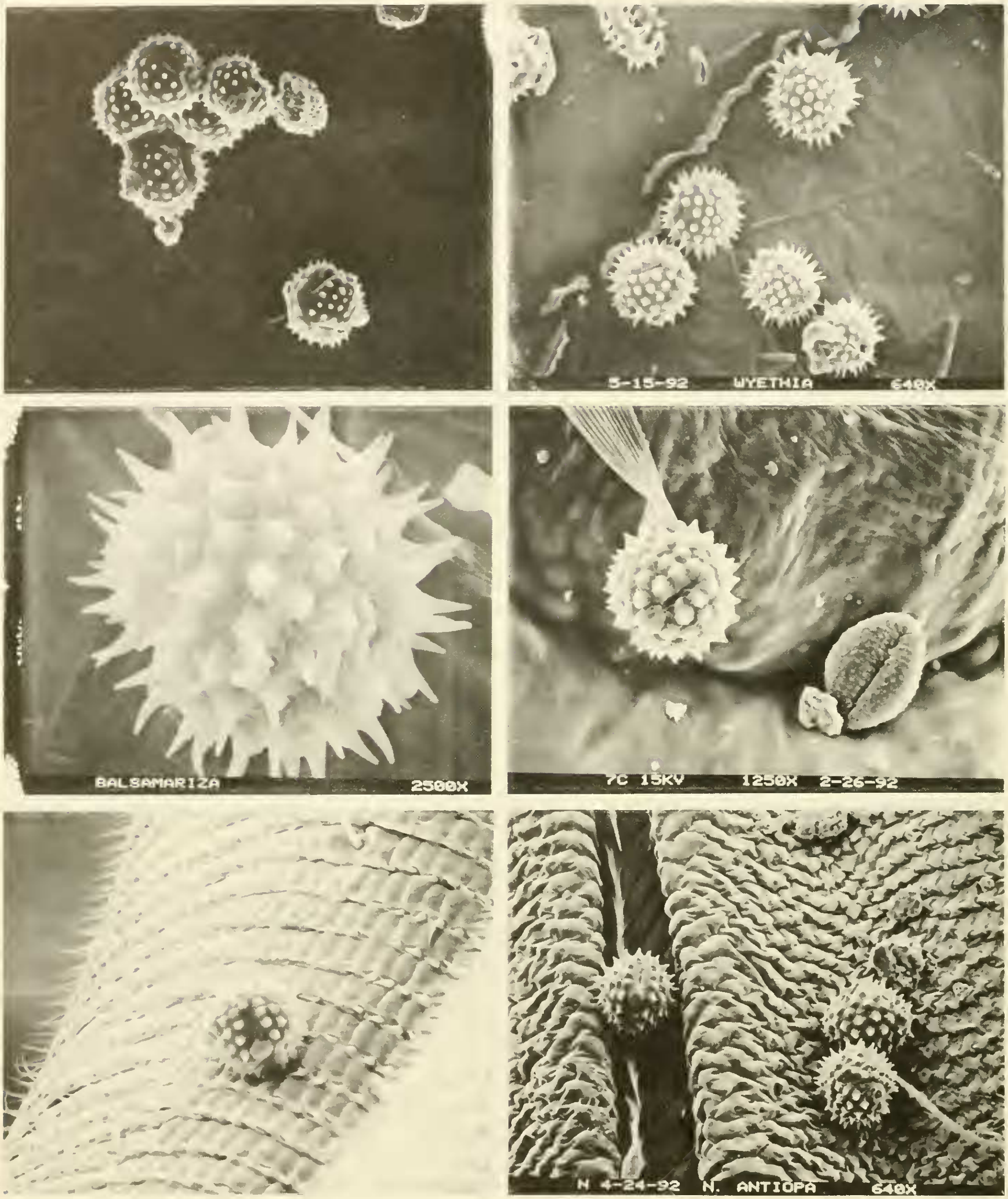
Most Holarctic *Hesperia* are univoltine (MacNeill 1964) although phenologically diverse even in a given location. In the northeastern United States, *H. metea* Scudder flies in early spring, *H. sassacus* Harris in late spring, *H. attalus* (W.H. Edwards) in summer, and *H. leonardus* Harris at the end of summer into autumn. In northern California there are distinctive populations of the *H. comma* L. complex that are univoltine from June to October in different localities (more than one species may be involved); *H. nevada* (Scudder) flies in early to midsummer at high elevation; *H. lindseyi* (Holland) is univoltine in late spring–early summer, slightly earlier than sympatric populations of the *comma* complex; only *H. columbia* (Scudder) is bivoltine, flying in foothill habitats in midspring (overlapping *H. lindseyi* a little) and again in early autumn (overlapping late "*comma*"). All Nearctic *Hesperia* appear to feed on perennial bunchgrasses, and all except *H. juba* have seasonal phenologies consistent with larval overwintering (albeit in different instars). One potential alternative explanation of the *H. juba* phenology, apparently falsified by this study, is that the nominal species *juba* consists of two wholly allochronic (spring and fall) univoltine populations, indistinguishable phenotypically. (A situation of this sort occurs in the *comma* complex on the western slopes of the Sierra Nevada, apparently involving sibling species that are, however, weakly phenotypically distinguishable.) The apparently universal sympatry of the putative populations argues against this hypothesis; if they were truly independent, surely there would be places where one occurs without the other.

The second flight of *H. juba* at Donner Pass coincides with peak flowering by the composite shrub rubber rabbitbrush, *Chrysothamnus nauseosus*. It and the polygonaceous subshrub *Eriogonum wrightii* Torr. ex Benth. (not visited by *juba*) are usually the only plants in flower at Donner then. *H. juba* visit this plant from midmorning until very late afternoon and are rarely seen anywhere else, or engaged in any activity but feeding. This contrasts with spring, when courtship, mating, and oviposition are all readily observed even though population densities are generally much lower. *Chrysothamnus* is visited by nearly all nectarivorous insects flying at that season, including the presumably hibernating nymphalids; late individuals of the larger fritillaries (genus *Speyeria*, Nymphalidae); the autumn-univoltine skipper *Ochlodes sylvanoides* (Bdv.); various lycaenid, pierid, and satyrid butterflies; bumblebees (*Bombus*) and honeybees (*Apis*) (Hymenoptera: Apidae); and many Diptera including Syrphidae, Bombyliidae, and Tachinidae.

Chrysothamnus is not a very prolific pollen producer, but we reasoned that its near monopoly on *H. juba* foraging in autumn and the near certainty that the last few feeding bouts prior to hibernation would have been on this plant make it an excellent candidate for persistent pollen detectable in spring.

METHODS

There seems to be only one published picture of *Chrysothamnus* pollen; its geographic origin is unspecified but likely is Utah (Solomon et al. 1973). We collected fresh pollen from *C. nauseosus* at Donner Pass in autumn 1991 (Fig. 1). We also collected fresh pollen from other composites whose pollen might cause confusion and which were in flower in spring 1992 at or near Donner Pass, whether or not they overlapped the first flight there. We obtained spring-collected specimens of *H. juba* from the Bohart Museum of Entomology, U.C. Davis (which has many from Donner Pass as vouchers of AMS's phenological and faunistic studies). We also collected spring 1992 specimens at Donner Pass. We did SEM searches for pollen following the methods of Courtney et al. (1982) with special attention to the facial cavity and basal portions of the proboscis. We did not attempt to identify non-composite pollens because we knew no non-composite whose phenology made it a potential indicator of overwintering.



Figs. 1–6. SEM studies: 1, *Chrysothamnus nauseosus*, Donner Pass, ix.1991, 640X; 2, *Wyethia mollis*, Donner, v.1992, 640X; 3, *Balsamorhiza sagittata*, Donner, v.1992, 2500X; 4, *Chrysothamnus* with another pollen, base of proboscis, *H. juba*, Donner, v.12.90, 1250X; 5, *Chrysothamnus*, proboscis, *H. juba*, Donner, vi.6.88, 1250X; 6, cf. *Chrysothamnus*, proboscis, *N. antiopa*, north Sacramento, v.1.88, 640X.

About 20 species of plants were in flower at Donner Pass during the 1992 spring flight; those visited by *H. juba* were *Phlox diffusa* Benth. (Polemoniaceae), *Calyptridium umbellatum* (Torr.) Greene (Portulacaceae), *Salix* sp. (Salicaceae), *Wyethia mollis* Gray, and *Taraxacum officinale* L. (Compositae). Of these, *Taraxacum* pollen is easily distinguished from *Chrysothamnus; Wyethia* is similar enough to require careful evaluation (see below).

RESULTS

At least 1 grain of *Chrysothamnus* pollen was found on 6/17 spring *H. juba* (Table 2), amounting to 25 of >374 grains examined (<7%). *Chrysothamnus* pollen was unevenly distributed among individuals: most grains were found on specimens bearing few pollen grains overall, and none or only one or two other pollen species. Specimens with heavy and diverse pollen loads tended to have no detectable *Chrysothamnus.* We interpret this as indicating that individuals just out of hibernation, which have had little chance to feed, are most likely to have carryover grains from the previous autumn. Subsequent feeding would either dislodge such grains or bury them in new pollen of other species, making them difficult to see. (Because fewer plants are in flower in early spring at the colder, drier east end of Donner Pass than in the west, spring specimens collected in the east are usually taken from bare soil and have very light or no detectable pollen loads in comparison to those from the west. Unfortunately, specimens taken before 1992 are merely labeled "Donner Pass.")

There are several composite genera presenting more or less similar spherical, tricolporate, echinate pollens that occur at or near Donner Pass. Several of these bloom at midsummer, in between the two flights of *H. juba*, and are not at issue. *Aster* and *Solidago* spp. often overlap the early part of the autumn flight. Since they never bloom in spring, any of their pollen found on *H. juba* would function as an indicator of hibernation. (Because they are so rarely still in bloom at the end of the flight, they are poor candidates for overwinter persistence. In fact, we have not detected them.)

Pollens of the genera *Balsamorhiza* and *Wyethia* (both Heliantheae) are sufficiently similar to *Chrysothamnus* as to require careful diagnosis. *Balsamorhiza sagittata* (Pursh.) Nutt. occurs on andesitic ridgetops overlooking the pass. It is uncommon and in most years blooms during the second half of the first flight. *Wyethia mollis* is very abundant and widespread. It blooms slightly later, usually in the last third of the first flight. These pollens were found on spring *juba* but are easily distinguished from *Chrysothamnus* even at low magnification by their more acuminate and differently spaced echinae (Figs. 2, 3).

TABLE 2. Occurrence of *Chrysothamnus* pollen grains on spring-collected *Hesperia juba* from Donner Pass.

Date of capture	Total pollen grains (all species)	*Chrysothamnus* pollen grains
vi.6.88	2	2
vi.6.88	0	0
v.12.90	10	10
v.12.90	10	0[a]
vi.1.90	10	10
v.8.92	15	1
v.8.92	>50	0
v.8.92	>100	0
v.8.92	7	0
v.8.92	2	0
v.8.92	4	0
v.8.92	2	1
v.8.92	10	0
v.8.92	20	0
v.8.92	7	0
v.16.92	25	1
v.16.92	>100	0
17	>374	25[a]

[a]One ambiguous grain on this v.12.90 specimen not counted as *Chrysothamnus.*

DISCUSSION

The concept of "pollen carryover" is familiar in pollination ecology (Handel 1983, Waser 1983), but there has been no incentive to look for truly long-term persistence. Wiklund et al. (1979) argued, based on studies of the wood white (*Leptidea sinapis* L. [Pieridae]), that butterflies are poor pollen vectors and that the lepidopteran proboscis is preadaptive for nectar "robbery." Flowers visited in Wiklund's study, however, were *Viola* (Violaceae) and *Lathyrus* (Leguminosae), which are normally pollinated by Hymenoptera and are neither "designed for" nor dependent on butterfly pollinators. Courtney et al. (1982) countered with data from several common Palearctic butterflies (including nymphalids reputed to hibernate), demonstrating not only significant pollen loads but relatively long pollen residence times (several days). From this they argued that butterflies, being relatively vagile, could be important agents of relatively long-distance pollination. Wiklund et al. (1982) countered that butterflies were still very inefficient as pollinators, and Tepedino (1983) noted that the usual, rapid decline in pollen viability with time would negate any dispersal advantage of butterflies as vectors. Venables and Barrows (1985) argued, based on studies of two North American species, that skippers did transfer pollen, but probably not very efficiently.

Chrysothamnus is visited by a great variety of insects and has a relatively generalized pollination syndrome. The relative efficiency of various visitors as pollinators is unknown, but seed set is typically heavy. Because the floral tube is long, the skipper must insert its proboscis deeply. The usual approach is from above, and many individuals dip forward far enough to bring the palpi and facial cavity into contact with the flower. We find occasional pollen grains on the legs and pelage as well as the mouthparts. Few approaches are made from the side, and it is unclear whether the proboscis could reach the nectar with this approach. We have observed *H. juba* using the forelegs to "groom" its head and antennae.

Tepedino's remarks on pollen viability are irrelevant to our study since, even if *Chrysothamnus* pollen remained viable overwinter, there would be no stigmas in spring to receive it.

We have found spherical, tricolporate, echinate, non-*Wyethia*, non-*Balsamorhiza* composite pollens on 5 of 8 presumably hibernated *Nymphalis antiopa* L. (Nymphalidae) selected haphazardly from the Bohart Museum's northern California series. As in *H. juba*, suspect pollen was most frequent on specimens bearing little pollen overall and few if any other species (Table 3). Some of these specimens are from low-elevation sites where *Chrysothamnus* does not grow, but other genera with similar pollens (*Aster, Solidago*, etc.) do. Shapiro (1986) argued, based on circumstantial, phenological evidence, that *N. antiopa* has a regular cycle of seasonal altitudinal migration in California. A more sophisticated study allowing us to discriminate among various summer- and autumn-flowering composite pollens west of the Sierra Nevada might permit a direct test of this hypothesis. Evidence in Table 3 is a credible, if not absolute, verification of the conventional wisdom that *N. antiopa* does indeed overwinter as an adult. It is inadequate to confirm migratory movement. (A European colleague has pointed out to us that *N. antiopa* reputedly does not visit flowers there. We have documented its visits to flowers in California by photograph as well as pollen studies.) Persistent pollen was used by Mikkola (1971) and Hendrix et al. (1987) to trace the sources of migrant Lepidoptera, including truly long-distance migrants.

There is a very remote possibility of secondary pollen transfer, i.e., that autumn pollens found on spring butterflies might have been acquired initially in autumn by other hibernating insects such as *Bombus* (Hymenoptera: Apidae) queens and redeposited in flowers where they were acquired by others. The abundance of grains in our study argues against this mechanism.

We have probably established that *Hesperia juba* overwinters as an adult, but not that

TABLE 3. Occurrence of *Chrysothamnus*-like pollen on spring-collected *Nymphalis antiopa* from high and low elevations in north central California. No attempt was made to discriminate among several *Chrysothamnus*-like pollens potentially available at low elevation, but all the genera bloom in late summer and autumn only. Note that the two vii.7.76 specimens from Sagehen Creek might be altitudinal immigrants from the late-spring emergence west of the Sierra (Shapiro 1986), while the vi.30.76 ones—based on phenotype and condition—probably overwintered locally.

Date and locality of capture		Total pollen grains (all spp.)	*Chrysothamnus*-like pollen grains
vi.30.1976	Sagehen Creek, Sierra County[a]	2	2
vi.30.1976	" "	7	7
vii.7.1976	" "	>150	0
vii.7.1976	" "	>100	0
iv.11.1977	Fairfield, Solano County[b]	13	6
iv.11.1977	" "	0	0
iv.13.1977	Willow Slough, Yolo County[b]	7	7
v.1.1988	North Sacramento, Sacramento County[b]	14	8
8		>293	30

[a]Elevation 1500 m; *Chrysothamnus* present.
[b]Elevation <100 m; *Chrysothamnus* absent.

this is its exclusive mode of overwintering. At lower elevations the time constraint on fall/spring larval development is less severe, and such a phenology becomes at least plausible. It would rarely be possible at Donner, but in rugged relief many microclimates occur, some of which might allow larval overwintering at least in some years. Some autumn females from Donner will lay fertile eggs, though they usually must be confined for at least a week before they do. Of 9 Donner females confined in autumn 1992, 3 laid a few fertile eggs and contained spermatophores; 2 contained mature or nearly mature eggs but no spermatophore; and 4 contained neither eggs nor a spermatophore at death. In 1992, 11 females were collected at Donner; of these 2 had mature eggs and none had spermatophores (Table 4). In addition, 3 were taken at Carson Pass, Alpine Co. (2700 m), 27 September 1992; of these 2 had neither eggs nor a spermatophore and the third had many eggs but no spermatophore. Interestingly, this last was being courted by a male when taken, the only courtship observed in autumn 1992. Perhaps females do not become attractive to males until they carry mature ova. Ford (1975) states categorically that nymphalids hibernate as virgins; clearly that need not be true for *H. juba*. (We attempted a small-scale experiment at carrying eggs overwinter 1991–92 at Donner, but all disappeared. We have also failed to carry third-instar larvae overwinter in refrigerators or freezers.) Spring females are almost always in breeding condition; 8 of 9 spring 1992 females dissected had both mature eggs and a spermatophore.

TABLE 4. Reproductive condition of 14 *H. juba* females collected in the Sierra Nevada in autumn 1992.

Date	Locality	Number of mature ova	Spermatophore present?
ix.2	Donner Pass	0	no
ix.2	"	0	no
ix.2	"	0	no
ix.18	"	0	no
ix.18	"	0	no
ix.18	"	3	no
ix.18	"	0	no
ix.18	"	13	no
ix.18	"	0	no
ix.18	"	0	no
ix.26	"	0	no
ix.27	Carson Pass	>25	no
ix.27	"	0	no
ix.27	"	0	no

H. juba is the largest hesperiine skipper in the Sierra and one of the two largest in California, but it is also the smallest butterfly known to hibernate as an adult in a climate with severe winters. A variety of relationships between body size and thermal biology has been postulated in Lepidoptera (Douglas 1986, Miller 1991). Naively, one might suppose that the heat-loss properties implied by surface/volume ratios might impose a lower limit of body size on butterfly hibernators. No hibernating insect can keep itself warm over winter by metabolic thermogenesis alone. Ability to hibernate must be related to the ability to get into a warm microclimate, lowering the freezing point by biochemical mechanisms, insulation, or some combination of these. Body size comes into play primarily in spring or autumn when the insect is active for part of the day but at risk for sudden, critical decrease of ambient temperature when the sun is obscured, or at dusk. A disadvantageous surface-to-volume ratio, uncompensated by insulation, could keep the insect from reaching shelter before it was immobilized by cold. We have watched nymphaline butterflies return to lava jumbles in late afternoon in the Sierra and quickly crawl to shelter, but we do not know where *H. juba* go.

Many insects much smaller than *H. juba* hibernate successfully in cold climates, but none is a butterfly. Those butterflies generally supposed to hibernate in the Holarctic (Nymphalidae: Nymphalini and Vanessini; Pieridae: *Gonepteryx* in the Palearctic and the Californian *Zerene eurydice* Bdv.) are remarkably uniform in size, though many butterflies of similar size do not hibernate. This is an interesting point, but we know too little of the energetics and physiology of butterfly hibernation to assess its significance. We merely note that *H. juba* is smaller than other known hibernators but is exceptionally large for a hesperiine skipper.

ACKNOWLEDGMENTS

This study was made possible by a University of California President's Undergraduate Fellowship awarded to AEB. We thank Rick Harris and Robert J. Munn for help with SEM; Robbin Thorp, Grady Webster, and Jim Doyle for discussion and suggestions; Owen

K. Davis and John Brooks for checking their SEM files for us; and C. Don MacNeill for comparing notes on *H. juba* biology and for acknowledging (by letter of 2 June 1992) that "I am now a believer in your suggestion that at least some *H. juba* overwinter as adults!"

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Received 19 January 1993
Accepted 4 August 1993